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Traumatic resin ducts in Alaska mountain hemlock trees provide a new proxy for winter storminess

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Key Points

- Traumatic resin ducts in the crossdated tree rings of subalpine mountain hemlocks record tree damage during winter storms in coastal Alaska.
- Warmer, windier winters that accompany strong Aleutian Low pressure systems result in more tree damage.
- Decadal-scale variability in North Pacific climate has impacted treeline ecosystems throughout this region.

Abstract

Winter is a critical season for land-surface feedbacks and ecosystem processes; however, most high-latitude paleoenvironmental reconstructions are blind to cold season conditions. Here we introduce a winter-sensitive, paleo-proxy record that is based on the relative frequency of tangential rows of traumatic resin ducts (TRDs) in the annual growth rings of mountain hemlocks (*Tsuga mertensiana*) growing near treeline in Southeast Alaska. Hemlocks produce a row of TRDs in the earlywood portion of their annual rings in response to cambial damage incurred during winter. Multi-decadal bouts of TRD production were followed by growth-leader replacement, reaction wood formation, and divergence in radial growth between storm-damaged trees and less exposed mountain hemlock forests. These patterns are consistent with TRDs being a response to tree damage caused by ice and snowstorms; a conclusion supported by the krummholz-like tree architecture at these sites. This relationship is further corroborated by significant correlations between our TRD record and the strength of the wintertime Aleutian Low (AL) pressure system that is linked to tree-damaging agents like wind, precipitation, and ice storm strength in Southeast Alaska. The combined TRD / krummholz architecture record indicates that abrupt shifts between strong and weak AL phases occurred every several decades since CE 1700, and that the 1800s had relatively long AL phases with heavy snowpacks. In addition to describing the magnitude and tempo of wintertime climate change in Northwestern North America, these results suggest that North Pacific Decadal Variability underlie the long-term dynamics of treeline ecosystems along the northeast Pacific coast.

Keywords

Dendrochronology; Tree Rings, Traumatic Resin Ducts, Treeline, Aleutian Low, North Pacific, Winter Storminess, Paleoecology

1. Introduction

Winter conditions play a key role in many ecosystem processes at high latitudes and in some cases determine the range distributions of biota [Battisti *et al.*, 2005; Tape *et al.*, 2010; Hagedorn *et al.*, 2014]. Over recent decades in the Arctic and Subarctic, air temperature has been changing most rapidly in winter [Walsh *et al.*, 2011; Cohen *et al.*, 2014]. To predict the future impacts of changing wintertime conditions, we need to know what winters were like before environmental record-keeping began, and how boreal ecosystems responded to past changes in winter climate. At the same time, reconstructions of past wintertime conditions can provide valuable new insights into the historical climatology of ocean-atmospheric modes of variability that are primarily expressed in the Northern Hemisphere winter (i.e. the effects of the El Niño Southern Oscillation and North Pacific Decadal Variability) [Trenberth and Hurrell, 1994; Wise and Dannenberg 2014].

The wintertime states of low-pressure systems that develop over the North Pacific and North Atlantic Oceans affect climate and weather across vast, downwind regions [Hartmann, 2015]. Prominent among these low-pressure systems is the Aleutian Low (AL), which is an important center of action for large-scale atmospheric circulation patterns [Rodionov *et al.*, 2007]. The strength and position of the AL affects the frequency, intensity, and trajectories of extratropical cyclones in the North Pacific [Trenberth and Hurrell, 1994; Mock *et al.*, 1998; Rodionov *et al.*, 2007; Zhu *et al.*, 2007], as well as the state of climate teleconnections like the Pacific North American pattern (PNA) [Overland *et al.*, 1999]. Variations in the AL are described by the North Pacific Index (NPI), which is the mean sea-level pressure within the region within 30°-65°N and 160°E-140°W [Trenberth and Hurrell, 1994]. The strength of the AL strongly affects the climate of Southeast Alaska (Figure 1), as indicated by negative correlations between the NPI and winter temperature, meridional winds, and, to a lesser extent, precipitation (Stronger AL = higher temperatures, stronger winds and more precipitation; Supporting Information, SI Figure 1). These changes in the distribution and flux of southerly heat and wind energy advected into the North Pacific help drive the sea-surface temperature anomaly patterns summarized by the Pacific Decadal Oscillation (PDO) index [Newman *et al.*, 2016]. At a larger spatial scale, the state of the AL affects droughts, floods, and wildfires in western North America [Cayan *et al.*, 1998; Seager *et al.*, 2015; Wise, 2016; Dannenberg and Wise, 2017], changes in earth-surface energy feedbacks like

Arctic sea-ice extent [Rodionov *et al.*, 2007], and the size and distribution of salmon runs along the Pacific coast [Mantua *et al.*, 1997].

The sensitivity of North Pacific climate variability to forcing by greenhouse gas concentrations is a topic of widespread concern (i.e. Gan *et al.*, [2017]). However, separating ‘natural’ from anthropogenic drivers of change requires detailed, pre-industrial records of past climate variability. A paleo-record estimating past variations of the AL can be very useful in this regard. Because the AL is most active in winter, finding paleo-records reflecting wintertime conditions is an important step forward for the investigation of the anthropogenic forcing on weather patterns. Unfortunately, records of wintertime conditions are rare in high latitude regions.

Tree rings can provide detailed paleo-records of climate at annual, and in some cases, sub-annual temporal resolution [Hughes *et al.*, 2010]. However, high-latitude trees are dormant in winter and so are most sensitive to warm season conditions [Wilson *et al.*, 2016]. A winter-sensitive record requires a geographic setting that is exposed to extreme winter conditions and contains a tree species whose annual rings bear witness to conditions outside the growing season. One such place is alpine treeline. Trees there can be exposed to heavy snowpacks that affect growing season length and ring-width patterns [Peterson and Peterson, 2001; Körner, 2012]. In addition, heavy snowpacks, ice abrasion and rime-ice loading can damage plant tissue and cause stem or branch breakage, which in turn can affect tree growth rates, architecture, wood morphology, and tree-growth characteristics [Pereg and Payette, 1998; Laberge *et al.*, 2001]. Secular changes in tree architecture, morphology and growth rates of treeline trees have been used to reconstruct changing snow conditions and winter storminess during the Little Ice Age in eastern Canada and elsewhere [Payette *et al.*, 1989; Lavoie and Payette, 1992; Payette *et al.*, 1994; Wooldridge *et al.*, 1996; Pereg and Payette, 1998; Laberge *et al.*, 2001; Kajimoto *et al.*, 2002; Tremblay and Bégin, 2005].

Here we introduce a new dendrochronological proxy for winter conditions based on the anatomical features of cross-dated tree rings from mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) growing near altitudinal treeline in the coastal mountains of Southeast Alaska. This paleo-record reveals how wintertime tree-damaging events in the North Pacific region have varied since CE 1700 during the climate fluctuations that accompanied the Little Ice Age and post-industrial warming [Wiles *et al.*, 2014].

2. Background: Tangential rows of traumatic resin ducts in tree rings

Conifers produce terpene-rich resins that serve as a physical and chemical defense against pathogens, insects, and decay [Zona, 2004]. Taxa in the Pinaceae family respond to such threats by enhancing the xylematic production of resin ducts [Krokene *et al.*, 2008], which are morphologically-distinct cells that transport resin to areas of cambial damage [Bannan, 1936]. Unlike the resin-rich Pinadeae sub-family, the Abietoideae subfamily including *Tsuga* spp. (hemlocks) do not routinely invest in cambial resin-duct production [Penhallow, 1907; Bannan, 1936; Wu and Hu, 1997; Zona, 2004], and only produce tangential rows of what are termed traumatic resin ducts (TRDs) within ~50 vertical cm and ~80 radial degrees from a cambial wound [Bannan, 1934; 1936; Krokene *et al.*, 2008; Schneuwly *et al.*, 2009a; 2009b]. Transversely viewed, TRDs appear as thick-walled, lignified, vacuous or pitch-filled vessels that occupy a portion or the entirety of individual tree rings (Figure 2c, d) [Jeffrey, 1904; Penhallow, 1907; Bannan, 1936; Wu and Hu, 1997]. The hormonal pathways that lead to resin duct production are initiated during the growing season a few days to weeks after damage occurs [Kuroda and Shimaji, 1983; Nagy *et al.*, 2000; Martin *et al.*, 2002], or at the onset of the following spring if the damage occurred prior to the growing season [Bannan, 1934; Fahn *et al.*, 1979; Kuroda and Shimaji, 1983; Zona, 2004; Stoffel and Hitz, 2008]. Resin ducts in the earlywood portion of the ring adjacent to the previous year's latewood indicate damage occurred prior to or at the start of the growing season. In this way, the position of resin ducts within an individual tree ring can be used to reconstruct the seasonal timing of damage [Stoffel and Corona, 2014]. Depending on the severity of the wound, proximity to cambial damage, and tree taxa, TRD production has been observed to persist for up to 1-3 years following injury [Kuroda and Shimaji, 1983; Phillips and Croteau, 1999; Nagy *et al.*, 2000; Zona, 2004; Stoffel and Hitz, 2008; Schneuwly *et al.*, 2009a; 2009b].

Previous studies have used the frequency and intra-ring position of resin ducts in tree rings to reconstruct long-term patterns of conifer tree damage from snow avalanches [Stoffel *et al.*, 2006; Casteller *et al.*, 2007; Butler and Sawyer, 2008; Stoffel and Hitz, 2008; Schläppy *et al.*, 2016; Favillier *et al.*, 2017; Ballesteros-Cánovas *et al.*, 2018], rockfalls [Stoffel *et al.*, 2005; Stoffel and Perret, 2006; Schneuwly *et al.*, 2009a; Sorg *et al.*, 2015], ice-damage or debris impacts due to flooding [Lepage and Bégin, 1996; Ballesteros *et al.*, 2010; Zaginaev *et al.*, 2016], other geomorphic disturbances [Stoffel, 2008; Stoffel and Bollschweiler, 2009], and

bark beetle attacks [DeRose *et al.*, 2017]. We know of no study that has used TRDs to reconstruct winter storminess.

There are several mechanisms whereby intense winter storms can damage the cambium on the trunk of a tree. First, strain and shaking of the stem due to heavy winds, and/or heavy snow and ice loads is known to cause damage to the cambial tissue anywhere along the stem [Fahn and Zamski, 1970; Gardiner *et al.*, 2016]. Second, ice abrasion from saltating ice crystals blowing across the snow surface can cause localized cambial damage [Payette *et al.*, 1994; 1996; Holtmeier and Broll, 2010]. Third, because well-spaced trees often have living foliage on lower branches that are subject to storm damage (Figures 2, 3), TRD production in the lower stem could also reflect canopy damage in open forests [Bannan, 1936; Krokene *et al.*, 2008].

3. Study Area

The sensitivity of this new proxy record relies on carefully choosing sampling locations where trees are chronically vulnerable to extreme winter conditions. We cored trees growing at three topographically exposed sites perched above the eastern Gulf of Alaska (Figure 1). Southeast Alaska is one of the stormiest, high latitude regions on Earth [Rodionov *et al.*, 2007]. (In the Aleut language, “Alaska” translates as ‘The object to where the action of the sea is directed’ [Orth, 1967]), At sea level in Yakutat, Alaska (Figure 1c), an average of 2.24 m of precipitation falls annually between October and March [Arguez *et al.*, 2012], and winter storms often coincide with intense winds that cause frequent wind throw in forests [Nowacki and Kramer, 1998]. Although there are no weather stations at our sites, which are located ~600 m above sea level (a.s.l.), snow and rain accumulation is assumed to be greater than at Yakutat; this inference is supported by the presence of 1- to 2-m-deep snowdrifts persisting into mid-May (Figure 3). Wintertime temperatures often fluctuate around freezing in Southeast Alaska at altitudes below 2000 m a.s.l. [Buma *et al.*, 2017], and these conditions are conducive to icing and heavy snow loads that are particularly harmful to trees and to human infrastructure [Nykänen *et al.*, 1997; Irland, 2000; Chang *et al.*, 2007].

The trees we sampled grow on uplifted marine terraces with paludified soils [Ugolini and Mann, 1979]. The study stands consist of widely spaced, mountain hemlock trees, many of

which are older than 400 years and possess complex growth forms indicative of repeated structural damage (Figures 2, 3). Upright, relatively undisturbed trees growing on nearby well-drained slopes suggest that saturated soil conditions are the initial cause of these trees' diminutive stature. Soils consist of 5-10 cm of peat overlying a shallow B/C soil profile. Most trees grow outside the margins of late-lying snow-patches (Figure 3b). The result is a parkland-like, elfin forest in which individual trees are highly exposed to wind and to physical damage during extreme weather events [Stathers *et al.*, 1994; Irland, 2000]. Trees at these sites have minimal pathogen or insect damage, which is characteristically minor in mountain hemlocks [Means, 1990]. The trees also show little sign of browsing from porcupines (*Erethizon dorsatum* L.).

Several field observations provide evidence these growth-suppressed trees are strongly affected by winter weather. The topographic positions of snowdrifts and the asymmetrical tree morphology both reflect the predominance of southeasterly winds in winter (Figures 2b, 3, SI Figure 1). The umbel-style architecture of taller trees (>3 m in height) indicates repeated, height-dependent pruning of their canopies by the combined effects of wind and ice-crystal scouring, in addition to breakage by loading under rime ice and wet snow (Figure 2a). Another common growth form is a small to medium-sized tree with numerous replacement leaders indicative of height-dependent, leader mortality (Figure 2b) [Hibbs, 1981; Payette *et al.*, 1989; Pereg and Payette, 1998]. Elfin or krummholz trees (<3 m in height) growing on and near exposed ridgelines possess “snow skirts” of undamaged branches and foliage near their bases that indicate the presence of a protective snowpack (Figure 3) [Payette *et al.*, 1989]. Directly above these skirts, many of these same trees have multiple leaders that are either killed or scarred by blowing ice crystals concentrated at the snow surface (Figure 3c). These observations suggest that tree architecture in the stands we studied is mainly a reflection of past winter conditions (i.e. Payette *et al.*, [1996]).

4. Methods

We collected 328 tree cores (0.5 cm-diameter) from 117 subalpine mountain hemlock trees growing at three sites on the western flank of the Fairweather Range of the St. Elias Mountains in Southeastern Alaska (Figure 1). To compare the TRD record from these highly exposed forests with less exposed forests, we also collected 50 cores from 25 western

hemlock trees (*Tsuga heterophylla*) growing in a lower elevation, less exposed forest ('Yellowlegs' in Figure 1). We cored trees within 1.5 m of their root crowns, and at least two cores per tree were taken 90° apart.

For the mountain hemlock trees, a subset of 34 krummholz trees were also cored through their replacement leaders, which are up-curved branches that take over the terminal growth position after an older leader is broken or damaged (Figure 2b). Together, the pith age and first episode of reaction wood in replacement leaders indicate when they took over the leader position (Figure 2b), and therefore provide a maximum-limiting age estimate for when previous leader mortality occurred. Pith ages of upright replacement leaders that persist for several decades to centuries indicate the onset of relatively heavy snowpacks that protects living tissue from ice scour. Subsequent episodes of reaction wood in replacement leaders were interpreted to indicate the occurrence of heavy winds, snow, and/or ice damage causing tree bending in the direction of prevailing winds (in this case southeasterly winds; Figures 2, 3) [Westing, 1965; Wade and Hewson, 1979; Schweingruber, 2012].

Tree cores were sanded with increasingly fine sand paper up to 1000-grit to reveal ring boundaries, TRDs, and reaction wood. Ring widths were measured digitally to 0.001 mm using high-resolution scans and uploaded to the computer program Coorecorder 8.1. Ring-width series were visually and statistically cross-dated using standard dendrochronological techniques [Holmes, 1983; Stokes, 1996] to ensure that each ring is assigned a calendar date (SI Table 1). We detrended ring widths using a negative exponential curve and a 200-year spline curve to preserve age-independent tree-growth patterns related to the TRD record. The individual tree-ring indices were averaged using a robust mean, and this time series is hereafter referred to as the storm-damaged ring-width chronology [Cook, 1985].

We identified TRDs under 10-50x magnification as cells that were large, thick-walled, and dark compared to the surrounding tracheid cells that make up normal growth rings in *Tsuga* spp. (Figure 2) [Schweingruber, 2007; Stoffel, 2008]. The TRDs we observed were always arranged in one continuous tangential row and occupied ~10-100% of the annual ring (Figure 2c, d). We only counted those TRDs located along the earlywood ring boundary (~95% of the total TRDs) because this is the type of TRDs known to reflect winter trauma [Stoffel and Hitz, 2008]. We identified reaction wood as being dark in color, having thick-celled tracheids, and having rings wider on the down-curve side than on the up-curve side of the same ring [Schweingruber, 2007].

Because taxa in the Abietoideae typically produce rows of TRDs within 1-3 years following physical damage [Bollschweiler *et al.*, 2008], we used a three-year bin of TRD occurrences in a tree for the index of annual winter storminess. For example, the TRD index from the year 1924 included all the TRDs observed in the 1924, 1925, and 1926 rings. Thus the value for each tree for a single year can range from zero (no TRDs) to three (each of the three rings in a bin including t , $t+1$, and $t+2$ possessed TRDs). When a single year had multiple TRDs in the same tree but in different cores from that tree, we counted them as one TRD for that year. The final annual TRD record is the number of TRDs in that three-year bin divided by the number of trees surveyed in those years (hereafter the TRD record). For example, if in the 1925 bin (rings representing 1925-1927) there were 10 total TRDs observed in the 100 trees surveyed for that year, then the TRD index was 10%. To explore what climatic conditions drove TRD production, we used Pearson's Correlation coefficients between the TRD record (percent of trees growing early-wood TRDs) with various climate observations and indices from the same growth year.

To explore what climatic conditions drove TRD production in these treeline forests, we used Pearson's Correlation coefficients between the TRD record (percent of trees growing early-wood TRDs) with various climate observations and indices from the same growth year. To determine whether the TRD record shared low frequency or decadal variability with climate indices we used two methods: 1) Cross-wavelet analysis following the methods of *Torrence and Compo* [1998]. For this analysis, we detected coherent cycles in the TRD, PDO, and NPI time series at a 0.05 significance level for periods from 3-30 years. This test for coherence was passed when the average wavelet power between the two time series was outside the 95% range of a random simulation of 1000 red noise time series with the same autoregressive characteristics as the target time series. 2) Regime-shift detection analysis following the methods of *Rodionov* [2004]. For this analysis we detected shifts in mean values using a cut-off value of 12 years (regimes that were <12 years required higher significant levels to identify a regime shift), a significance level of 0.1, and a Hubner's outlier weighting of two for both the TRD, PDO, and NPI time series. We then excluded regimes <8 years to avoid high-frequency variations affecting regime-shift identification.

We also assessed whether there was an age or ring-width bias in the rates of TRD production because such a bias would influence paleoenvironmental reconstructions based on TRDs. We found that TRDs are less likely to occur in young trees (<300 years old). This pattern is

contrary to the lowered TRD production rates with age observed in other conifers [Larson, 2012], and we think this is due to the younger trees at our study sites being smaller, less exposed, and protected by snow cover in winter. To compensate for this age effect, we adjusted TRD counts from relatively young trees by fitting a general additive model to a histogram of TRD occurrence by age organized into 20-year-bins (SI Figure 2). We identified where the slope of this curve between two age bins was not significantly different from zero (non-zero slope ended at the 300-320 year age bin), and calculated the ratio between the probability density of each age bin less than 300 years to that occurring at 300 years. This ratio was then used as a multiplier to weight each TRD that occurred in a tree when it was <300 years old (SI Figure 2). To further assess this potential age bias in our final chronology, we calculated TRD records for trees when they were younger than 300 years and when they were older than 300 years.

Another potential source of bias is that wider annual rings may be more likely to contain more TRDs. To check for this potential bias, we compared the distribution of raw ring widths and standardized ring widths of rings that had TRDs to those without TRDs using a Kolmogorov-Smirnov test [Lilliefors, 1967]. We also tested whether aspect in relation to prevailing winds affected TRD occurrence within a tree by comparing rates of TRD occurrence (total TRD / total ring number) in 59 south-facing (windward) cores with their north-facing counterparts from the same level of the same trunk and conducting a paired Student's T-Test. Finally, to determine how tree-damaging episodes affected forest growth, we compared the ring-width indices of the storm-damaged trees from this study with the February-August (Feb-Aug) air temperature reconstruction from the Gulf of Alaska region [Wiles *et al.*, 2014], which is based on upright trees that experienced less storm damage. We used a 25-year running correlation between these two calendar-dated records to determine when storm-damaged trees were sensitive to the regional Feb-Aug air temperatures, and when they were insensitive to these inter-annual climate patterns. During times of lowered correlations, we infer that some other environmental factor besides Feb-Aug temperatures intervened to limit the growth of these storm-damaged trees.

5. Results and Discussion

5.1 The TRD record

A 315-year TRD record (CE 1700-2014) was produced based on the relative frequency of TRDs at the three storm-exposed sites (Figure 4). Agreement between ring-width patterns was high among trees based on cross-dating statistics (SI Table 1), allowing us to confidently assign calendar dates to the TRD record. In general, multi-decadal peaks of TRDs alternate with periods when relatively few trees produced TRDs (Figure 4). Overall, 0.88% of all rings surveyed in individual cores had early-wood TRDs (SI Table 2). The mean TRD index is 7% between CE 1700 and 2014 (Figure 4). This ranged from 0% to 25% of the trees surveyed (Figure 4). In a low-elevation, less exposed stand of western hemlock, TRDs occur in trees at less than half the rate as observed at the high-elevation sites (0.38% of all rings surveyed in individual cores) ('Yellowlegs' site in Figure 1, SI Table 2). This provides further evidence that TRD production is not a random process in space and time, and, as is the case in related taxa [Stoffel, 2008], TRD production is triggered by damage to a tree's cambium, which occurred more frequently at the more exposed sites.

5.2 Distribution of TRDs within trees

Only 12% of TRDs were observed in the same three-year bin somewhere else in the same tree. This suggests that mechanical damage in just a portion of the cambium is responsible for the presence of the TRDs. We found no bias in TRD orientation in north- vs. south-facing cores from the same trees (T-Test p-value 0.94), and no height-dependent bias in trees cored at different heights (Pearson's Correlation between height a core was taken and percent of rings that had TRDs: $R = 0.05$). These patterns are consistent with prior observations that TRD production is localized within ~50 vertical cm and ~80 radial degrees of cambial damage in *Tsuga* spp. and other members of the Abietoideae [Bannan, 1934; Schneuwly et al., 2009a; 2009b]. Because of this localized TRD occurrence, and our 2-6 cores per tree, it is possible that our cores missed some TRDs in certain trees. Nonetheless, our approach of randomly sampling this highly exposed forest allows us to gauge the relative rate of TRD production and tree damage over time.

We found that younger trees were less likely to be damaged and to produce TRDs than trees older than 300 years (SI Figure 2). As noted above, we correct for this bias by weighting TRD occurrence in trees when they are <300 years old. This age effect may arise because younger trees are short enough to be largely covered by the snowpack and hence protected from the elements through much of the winter [Kajimoto *et al.*, 2002]. When young trees are above the snowpack, snow loading also inflicts less strain on younger trees because their smaller, more flexible branches can shed heavy snowfall [Marchand, 2014]. This strain is known to drive cambial dieback at the base of the stem as well as near the canopy [Petty and Worrell, 1981; Stokes, 1999; Spatz and Bruechert, 2000]. It is important to note that the main features of our TRD record do not change with or without this age-weighting (blue vs. gray polygons in Figure 4), and the TRD record based on trees that are <300 years old is positively, albeit weakly, correlated with the record based solely on >300-year-old trees ($R=0.33$) (SI Figure 3). Therefore, the broad patterns of TRD production are non-age dependent.

Results of Kolmogorov-Smirnov tests indicate that TRDs occur preferentially in growth rings that are relatively thin (SI Figure 4). However, after detrending ring width for tree age, the standardized ring widths of those rings containing TRDs are not significantly different from those without TRDs at the 95% confidence level (SI Figure 4). This suggests that TRD distribution is affected more by tree age than by ring width because raw ring widths are larger in younger trees because of age-related growth trends. We interpret this to mean that the occurrence of TRDs is not dependent on standardized ring width, which in mountain hemlock trees in Southeastern Alaska is known to be sensitive to mean spring and summer temperatures [Wiles *et al.*, 2014].

5.3 TRDs compared with other tree damage indicators

We found that during periods with lower frequencies of TRDs, tree regeneration indicators, such as leader replacement and reaction wood, were more common in the studied trees. For instance, at the Justice Terrace site (Figure 1), high rates of replacement-leader recruitment occurred between CE 1810-1850 when relatively few trees generated TRDs (Figure 5). This period of new leader recruitment followed two prominent peaks in TRDs during the early and late 1700s, and likely represents a deeper snowpack that provided protection while

krummholz trees grew replacement leaders to relatively higher positions, which were then above the ice-scour zone in later years with thinner snowpacks. Similarly, more replacement leaders grew reaction wood during periods when relatively few trees laid down TRDs in their annual rings (Figure 5). The alternations of decades with heavy tree damage (i.e., TRDs) and enhanced tree regeneration (i.e., leader replacement and reaction wood) is consistent with TRDs being an indicator of winter tree damage to treeline forests in Southeast Alaska.

In addition to the effects that winter weather had on tree damage, regeneration, and architecture at these treeline sites, tree-ring widths responded as well. The 25-year running correlation between the storm-damaged RWI and the Feb-Aug temperature reconstruction are insignificant ($R < 0.38$, $p\text{-value} > 0.05$) during the time when most replacement leaders began growing upright between 1810 and 1850 (Figure 5). The running correlations are also lower during some episodes when TRDs are more common (1720-1740, 1770-1785, 1900-1945, and after 1980) (Figure 5). We hypothesize that: 1) The enhanced snowpack that likely allowed a heightening of the krummholz tree canopy in the early 1800s caused ring-width patterns in the storm-damaged trees to diverge from temperature-sensitive tree-ring chronologies elsewhere in the region. And/or 2) Enhanced leader damage in the 1700s caused the tree -damaged RWI to be less sensitive to climate during the initial phase of regeneration between CE 1800 and 1850.

Further corroborating the TRD and tree-architecture records, ring widths exhibit periods of declining growth during and immediately after some periods of peak TRD production (grey bands in Figure 6). This includes declining growth trends following TRD peaks in in the 1720-40s, 1780-90s, 1920-40s, and after the 1970s. We hypothesize that these growth deviations and/or lack of Feb-Aug temperature sensitivity reflect lowered resource allocation to radial growth as a result of: 1) canopy damage that reduced the trees' photosynthetic capacity during warmer summers [Smith and Shortle, 2003] and/or 2) reduced radial growth due to the shifting of energy allocations to regeneration (i.e. reaction wood, wound healing, root strengthening) and damage-reaction pathways (i.e., TRDs) following winters when storm damage was sustained [Zona, 2004]. Similar growth-reduction deviations have been observed following ice storms in eastern North America [Warrillow and Mou, 1999; Hooper et al., 2001; Lafon and Speer, 2002; Smith and Shortle, 2003]. Growth-reduction also occurred among treeline black spruce in Quebec after a reduction in snowpack depth during the Little Ice Age [Payette et al., 1989; Lavoie and Payette, 1992; Payette et al., 1994; 1996]. Clearly,

wintertime processes can have strong impacts on summertime growth processes in high-latitude forests.

In summary, our field observations and tree-ring data strongly suggest that changes in the abundance of TRDs in the annual rings of subalpine mountain hemlocks provide a dependable proxy record of the severity of past winter storm damage. The lines of evidence include: (1) More TRDs are found in trees growing in more topographically exposed sites. (2) Bouts of heavy TRD production alternate with anatomical features associated with tree regeneration occurring during non-stormy times. (3) More TRDs are produced as a tree gets older, taller, and more exposed to wind, snow and ice damage. (4) Radial growth rates and sensitivity to summertime climate sometimes suffer after winters when TRD production indicates severe winter damage.

5.4 Climate correlations

We have not used the TRD record to construct a quantitative reconstruction of climate, as is commonly done using ring-width indices [Hughes *et al.*, 2010] in part because the TRD record consists of binary data (TRD presence/absence) instead of continuous data like in ring-widths. Thus, each TRD episode represents the crossing of some threshold of physical damage that prompts a biological response in the tree. Thus it is unlikely that the TRD record is explained by any one climatic factor in a linear fashion. Nonetheless, by combining these binary measurements into a composite record of the percent of trees damaged in these stands, we can explore correlations with climate factors to reconstruct an informative, *qualitative* record of winter storminess near treeline in the study area.

Due to the remoteness of our study sites, we are relegated to comparing the TRD record with region-wide and reanalysis-based climate summary indices. The annual (three-year binned) TRD record is positively, but weakly correlated with regional annual mean monthly winter temperatures and mean monthly meridional wind speeds (SI Figure 5). The annual TRD record also correlates significantly with instrumental data from Yakutat including the annual mean monthly temperatures from January to May ($R=0.36$; CE 1917-2014) and the annual number of winter (Nov-Mar) days with a daily mean above 0°C ($R=0.44$; CE 1948-2014). These climatic connections are logical because the likelihood for tree damage increases when

winters are windier and when air temperatures are warmer, which in this case means near the freezing level (mean Nov-Mar air temperatures in Yakutat 1946-2017: -1.5°C ; 95% range: -5.3° to 2.2°C). Storms occurring when air temperatures are near freezing can be harmful to trees for several reasons: 1) Winter precipitation events that begin near 0°C followed by a cooling trend result in higher snow-loads on trees because warmer air masses hold more moisture and produce snow with higher moisture content [Schmidt and Gluns, 1991], which makes trees vulnerable to damage by straining branches and/or being damaged by subsequent wind events. 2) Warmer temperatures also make it more likely for winter ice storms to encase exposed branches and foliage in rime ice, which is one of the main forest disturbance agents in regions where winter temperatures fluctuate around the freezing point [Changnon, 2003]. 3) A higher density of rime ice is deposited when temperatures are near freezing; whereas less adherent, soft rime is deposited at temperatures $< -8^{\circ}\text{C}$ [Baranowski and Liebersbach, 1977; Makkonen, 2000]. In summary, warmer winters in Southeastern Alaska make tree-damaging events more likely to occur, and this is reflected in the TRD record.

5.5 Tree damage is related to shifts in the North Pacific climate indices

Based on the likelihood that a combination of climate variables underlie tree damage at our study sites, we explored the relationship between large-scale climate indices and the TRD record. Climate summaries like the wintertime NPI and PDO are often correlated with many of the climatic variables relevant for tree damage in Southeast Alaska (temperature, wind, precipitation) (SI Figure 1) [Trenberth and Hurrell, 1994]. Based on the changing frequency of annual TRDs, the trees we studied had a higher likelihood of being physically damaged during synoptic conditions associated with a relatively strong AL (negative NPI) (annual Nov-Mar NPI \sim TRD record: $R = -0.34$; CE 1900-2014) (Figure 7) and a relatively positive PDO pattern (Figure 7, annual Dec-May PDO \sim TRD record: $R = 0.41$; CE 1900-2014). As a result, during springs following strong AL winters (negative NPI) and with a positive PDO, more subalpine mountain hemlock trees responded to the stress and damage of severe winter weather by producing TRDs than during springs following winters with a comparatively weak AL (positive NPI) and negative PDO (Figure 7). This connection is logical because: 1) Weather-station data show that a strong AL and a positive PDO are accompanied by warmer, windier, and rainier winters in Southeast Alaska [Mock *et al.*, 1998; Neal *et al.*, 2002], and 2) the TRD record has a similar multi-decadal phasing as the AL and PDO (Figure 7). In

support of this, average cross-wavelet analysis of the annual TRD record and the wintertime NPI/PDO had a significant power in the 16-21 year frequency (SI Figure 7). In addition, most of the regime shifts identified in the NPI and PDO records were within four years as those identified in the TRD record (Figure 7). Overall, decadal bouts of heavy TRD production in prehistoric times likely coincided with decades when the Aleutian Low was stronger and the PDO was positive.

If the relationship between TRD production and these regional ocean-atmospheric modes of variability is stationary, we can conclude that the bimodal, multi-decadal AL/PDO regimes that are prominent in the post-CE 1900 instrumental period have occurred throughout the entire TRD record from CE 1700 to 2014 (Figure 4). We can also conclude that the 20th century had a similar tempo and magnitude of storm damage as the 18th century (Figure 4), while in contrast the 19th century had longer, more variable episodes of tree damage and regeneration representing shifts in the NPI/PDO (Figure 4, 5). A particularly interesting time period for NPI/PDO dynamics was between CE 1800 and 1850, when the krummholz canopy rose, and ring-widths in storm-damaged trees diverged markedly from their temperature-sensitive counterparts, which may represent a particularly weak AL phase (low TRD numbers), and the beginning of a multi-decadal episode with heavy winter snowpacks.

5.5 Comparison with other records of regional climate

Paleo-reconstructions of North American teleconnection patterns and water resources governed by the AL generally agree with the temporal pattern of tree damage recorded by TRDs since CE 1700. First, correlations between the annual TRD record and the annual February-September mean temperature reconstruction based on mountain hemlocks in the Gulf of Alaska sites is significant (Figure 6; $R=0.39$; CE 1700-2010) [Wiles *et al.*, 2014]. In addition, the annual TRD record is weakly correlated ($R=0.27$) with a tree-ring- and varved lake-sediment-based reconstruction of the wintertime PNA that integrates far afield proxy records from the American Southwest and New England [Liu *et al.*, 2017]. This is expected because a more positive PNA pattern in the instrumental record is associated with a stronger AL [Overland *et al.*, 1999] and thus with more tree damage in Southeast Alaska. Also, as expected from the contrasting influences of AL intensity on winter storminess between Southeast Alaska and the Pacific Northwest (Washington and Oregon), the low-frequency

TRD record corresponds well with the low-frequency growth variability among trees at high-elevation sites in Washington and Oregon where growth rates are limited by the amount of spring snowpack (SI Figure 8) [Peterson and Peterson, 2001]. Overall, these far-afield correlations suggest that, in addition to being affected by past shifts in the AL and PDO, the TRD record has implications for cold season moisture variability across large regions of downwind North America.

In contrast, the Wise and Dannenberg, [2014] reconstruction of the cold season 500 mb height field over the North Pacific shows poor agreement with our TRD record associated to the AL. This could be due to varying seasonal sensitivities of the tree-ring chronologies or because of the lack of tree-ring data from sites above $\sim 50^{\circ}$ N in their reconstruction. In addition, the TRD record does not indicate a multi-century strengthening of the AL since the mid-18th century as is inferred from the Mount Hunter and Mount Logan ice cores [Osterberg *et al.*, 2017; Winski *et al.*, 2018] (Figure 4-5), but this could be because we do not have a pre-1700 TRD period to compare with at this time.

5.6 Impacts of climate change on treeline forests in Southeastern Alaska

The dynamics of alpine treelines are often governed by changes in the climatic variables that control the upper limits of tree growth and tree-seedling establishment [Körner, 2012]. In general terms, changes in summer temperatures are often invoked as the drivers of ecological changes at treeline; an interpretation supported by treeline expansion during warm periods in the early Holocene [MacDonald *et al.*, 2000; Mann *et al.*, 2010], during the Medieval period [Hiller *et al.*, 2001], and during the 20th century [Kullman and Öberg, 2009]. But how does treeline behave in hyper-maritime locations where long-term climatic trends have been minor relative to the abrupt decadal climatic shifts associated with ocean-atmospheric regime shifts [Wendler *et al.*, 2016]? For example, frequent multi-decadal shifts and cycles of winter climate in the coastal regions of Southeast Alaska create more complicated dynamics for treeline responses than simpler, directional shifts in summer climate. In our study area, a strong phase of the AL that persists for several decades may enhance tree damage and compromise growth and recruitment in the stands. On the contrary, more protected treeline sites that make up most of the dendroclimatology record in this region might respond to this same strong AL phase with favorable growth and perhaps forest expansion as a result of

warmer springs and summers [Wilson *et al.*, 2007; Wiles *et al.*, 2014]. We hypothesize that, in addition to monotonic climate change, the nature of these decadal-scale shifts in climate have been a primary driver in past treeline dynamics in the hyper-oceanic regions of northwestern North America.

Conclusions

Existing high-latitude paleo proxies are often blind to the winter season. The relative frequency of traumatic resin ducts (TRDs) formed in subalpine mountain hemlocks growing in hyper-maritime, treeline stands in Southeast Alaska provides a record of tree damage during winter. TRDs record local cambial damage in response to heavy wind damage and/or ice scour on tree stems and branches. TRDs were less likely to occur when trees are younger, smaller, and protected under the snowpack during winter. At the sites we studied, there is no apparent ring-width, height, or aspect bias for TRD occurrence. Radial growth rates diverge from growth rates in more protected and lower elevation mountain hemlock forests during episodes of increased TRD production and inferred heavy snowpacks, suggesting that winter processes can also affect growth rates at these sites. During winters when the Aleutian Low pressure system is particularly strong, warmer temperatures and enhanced southerly winds create icy, stormy conditions that increase the likelihood of tree damage and TRD production. This paleo-environmental perspective on the strength of the Aleutian Low and the phase of the Pacific Decadal Oscillation indicates that the bi-modal patterns of North Pacific Decadal Variation known from the post-1900 instrumental record also occurred back to at least CE 1700. We hypothesize that these shifts in wintertime climate may be a primary driver of treeline dynamics along the North Pacific coastline. This new tree-ring proxy provides a measure of winter storminess that can be applied to other synoptic patterns or weather events where similar tree taxa produce TRDs in response to extreme weather events.

Acknowledgements and Data Sources

All instrumental and reanalysis climate data presented here was downloaded from <https://climexp.knmi.nl/>. All paleoenvironmental data that was compared with the data presented here was downloaded from <https://www.ncdc.noaa.gov/data-access/paleoclimatology-data>. New data generated by this study and presented in this paper including the tree-ring-width records, traumatic resin duct frequency, and reaction wood frequency can be found in the supplemental material of this manuscript, and will eventually be available in the noaa.gov paleoclimatology dataset. This work was funded by the Climate Center at Lamont-Doherty Earth Observatory at Columbia University (LDEO) as well as the National Park Service. The LDEO Postdoctoral Fellowship funded BVG's time. APW, GCW, and LAH received funding from the National Science Foundation (AGS-1703029, AGS-1502186, PLR-1504134, AGS-1502150, OISE-1743738, and PLR-1603473). We thank Rowan Sharman, Philip Wilson, and Virgil E. Purchase for help in the field, and Kyle Hansen for lab assistance. This project benefitted from expert piloting by Gary Thompson of Admiralty Air, and logistical support by Louis Sharman. Discussions with Greg Streveler, Bruce Finney, Alexey Kaplan, Edward Cook, and Brendan Buckley contributed to our thinking on this project. We acknowledge the pioneering tree-ring work of Gordon Jacoby who collected the samples at the 'Dwarf Trees' site during a no-doubt stormy November in 1979. This is LDEO contribution xxxx.

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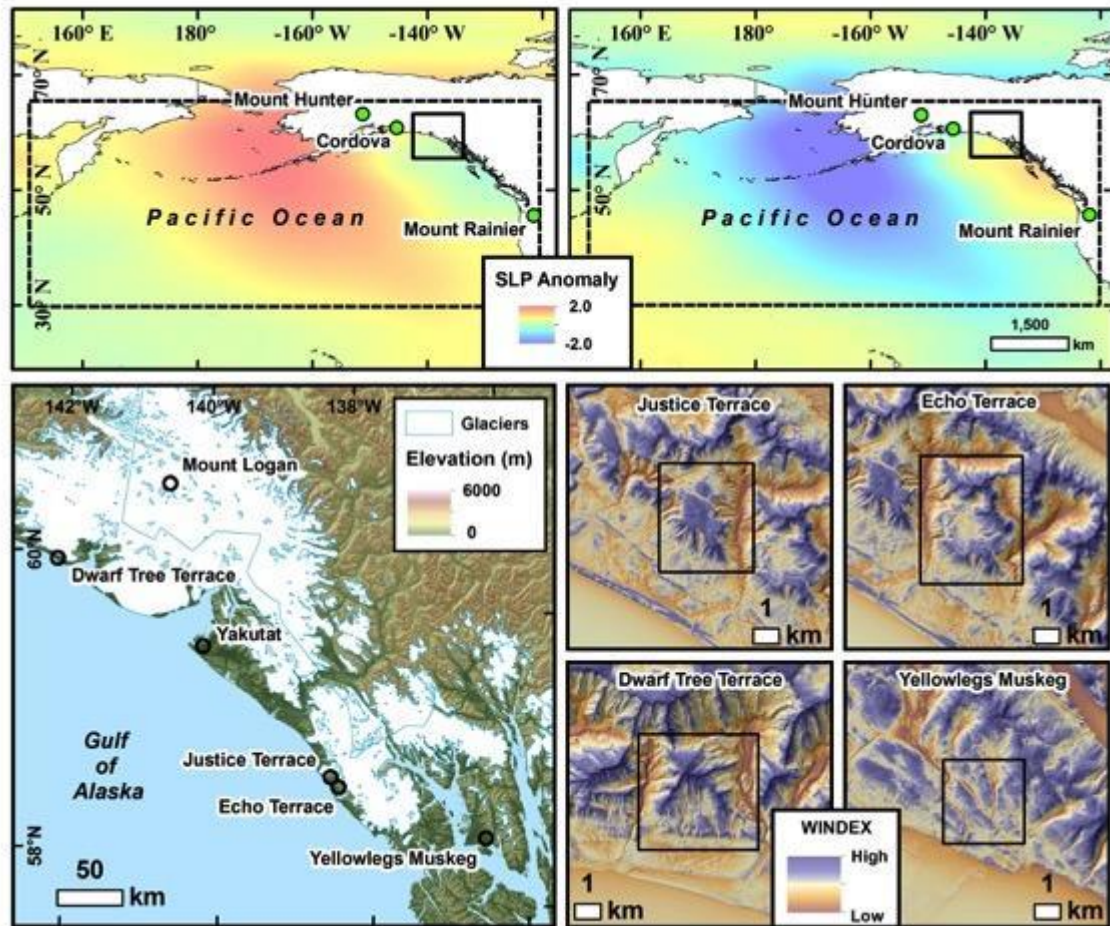


Figure 1. Top: The Northeast Pacific region showing locations mentioned in the text and mean winter (Nov-Mar) sea-level pressure (SLP) anomaly patterns [Trenberth and Hurrell, 1994] during relatively a) weak (1948-1976), and b) strong (1977-2005) states of the Aleutian Low. c) Map of the Gulf of Alaska region with study sites. d) Topographic exposure index (WINDEX) is overlaid on the hillshade of the four storm-damaged tree sites [Boehner and Antonic, 2009; Gerlitz et al., 2015]. Trees were sampled on flat, exposed terraces within each box.

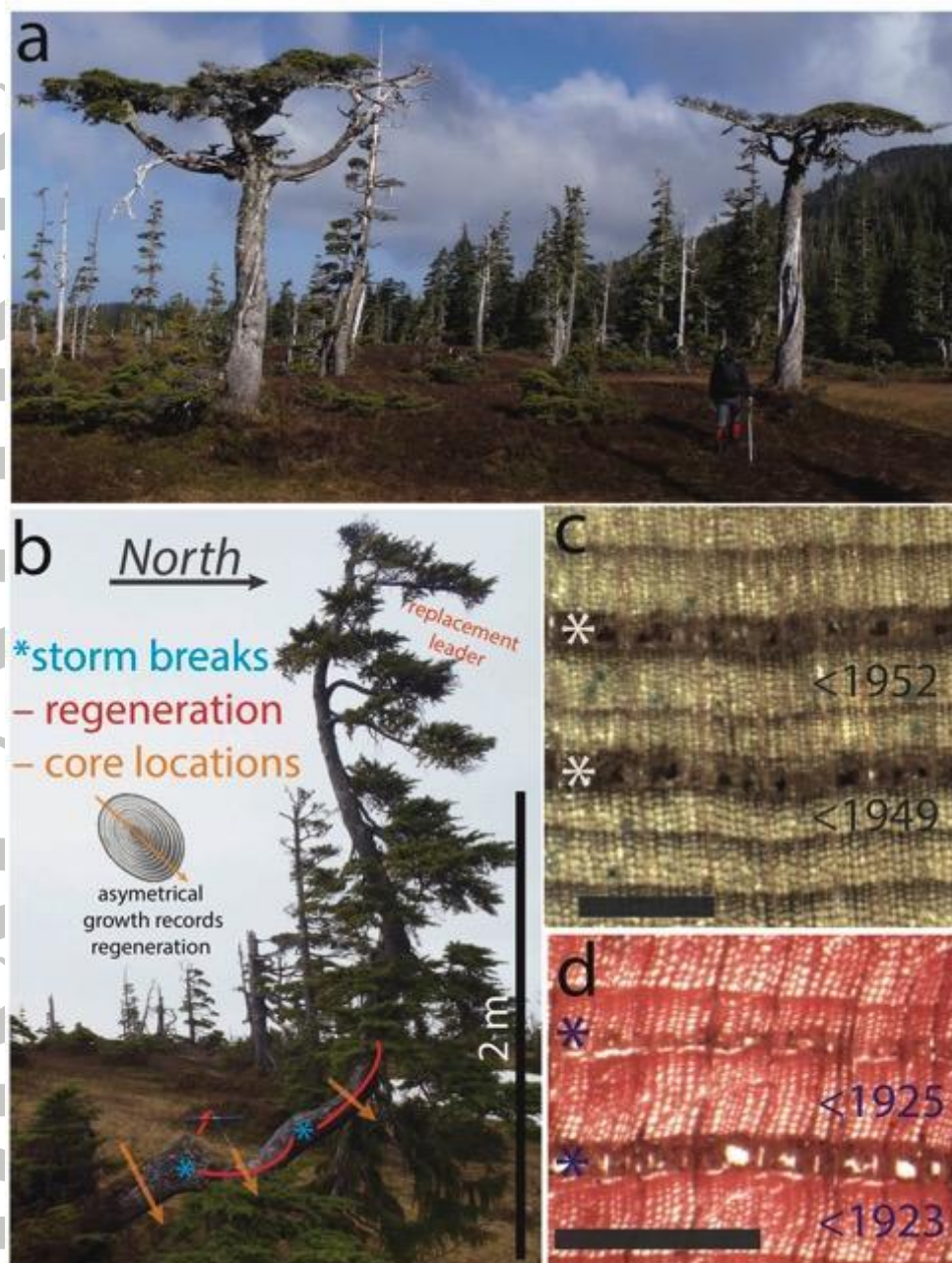


Figure 2. Upright (a) and krummholz (b) mountain hemlock trees growing near treeline at the Justice Terrace site. The changing morphology of krummholz trees record episodes of leader replacement by upturned branches following storm damage. c) Photomicrograph of tangential rows of traumatic resin ducts (TRDs) marked with stars in cores taken near the base of upright trees. d) Photomicrograph of TRDs in a thin-sectioned core marked with stars. Traumatic resin ducts are found throughout the trunks of krummholz trees. Scale bars in c and d are 0.5 mm.

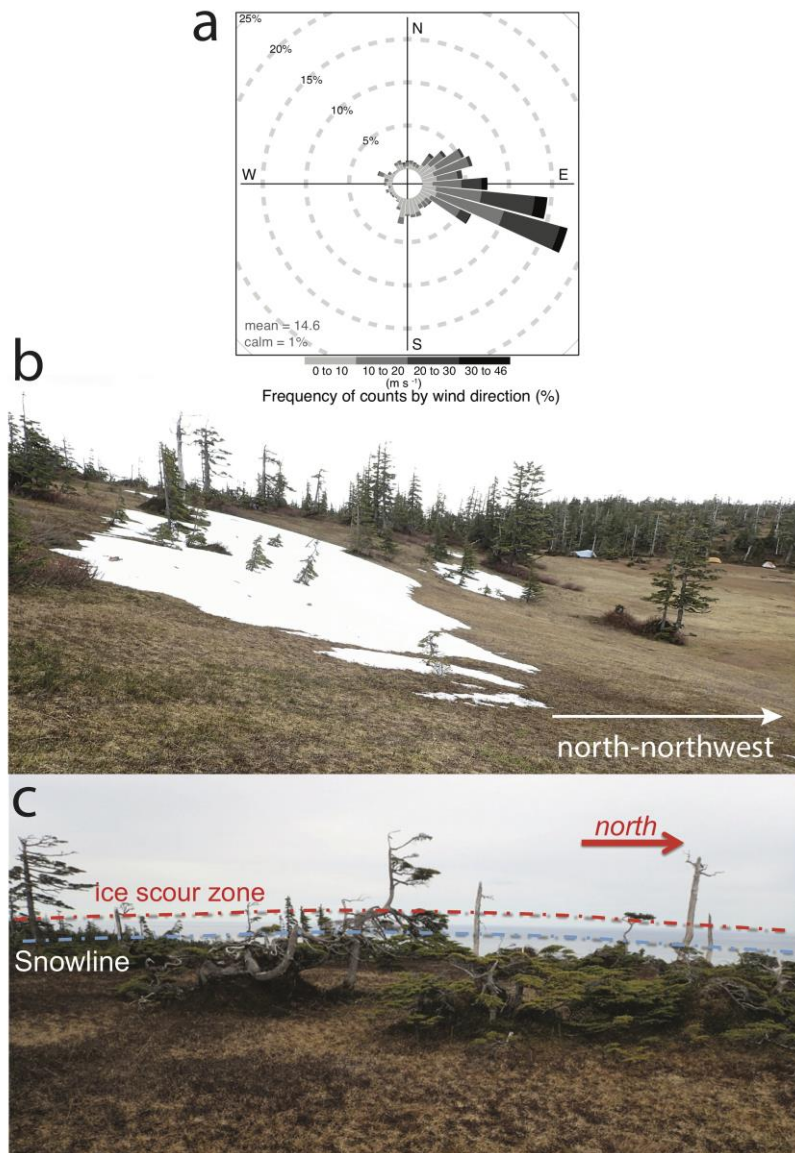


Figure 3. The architecture and distribution of subalpine mountain hemlocks at the study sites are dictated by winter weather. a) Two-minute maximum of daily November-March wind speed and direction recorded at the Cordova, Alaska airport (see Figure 1) between November 1999 and March 2017. b) Justice Terrace site in mid-May 2017. The melting snowdrift covers much of this lee slope during the winter, and its persistence into the growing season excludes most trees. Lingering spring snow on north- and northwest- facing slopes is partly due to the prevailing winter winds from the southeast and partly due to reduced insolation due to aspect. Blue and yellow tents seen in the background provide scale. c) Krummholz trees on the exposed ridge of the Justice Terrace are protected from wind and cold by the winter snowpack. During ice storm events, canopies projecting immediately above the snowpack are damaged by saltating ice particles and broken by loading under rime ice and snow.

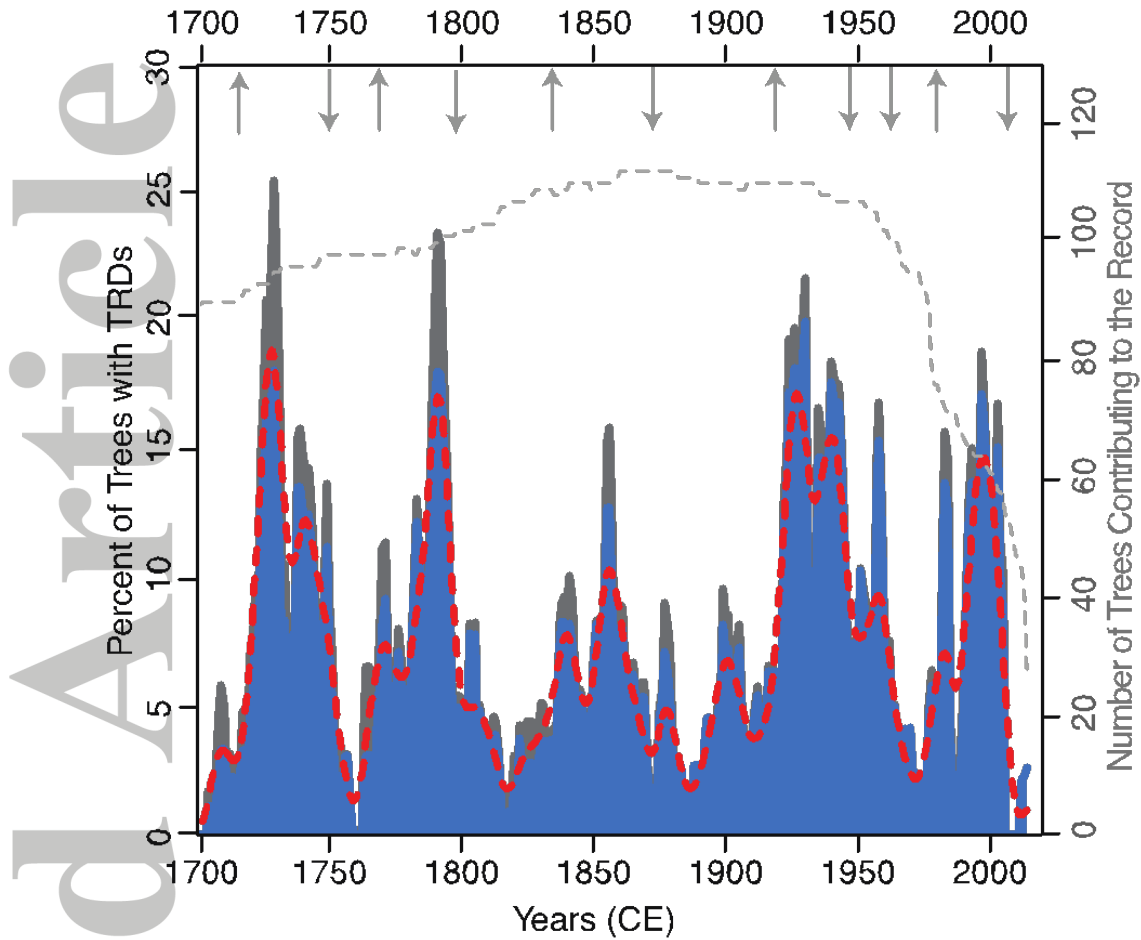


Figure 4. The relative frequency of TRDs (raw-percentages; blue polygon, age-weighted; gray polygon) in cross-dated tree rings from CE 1700 to 2014. Dashed gray line and right axis notes the number of trees contributing to the record over time. Thick red line is a smoothed spline with a 0.4 alpha smoothing parameter. Arrows at top denote the timing and direction of regime shifts in the mean of the weighted TRD time series identified using *Rodionov*, [2004] (significance level: 0.1; regime cut-off length: 15 years; Huber's outlier weight parameter: 2).

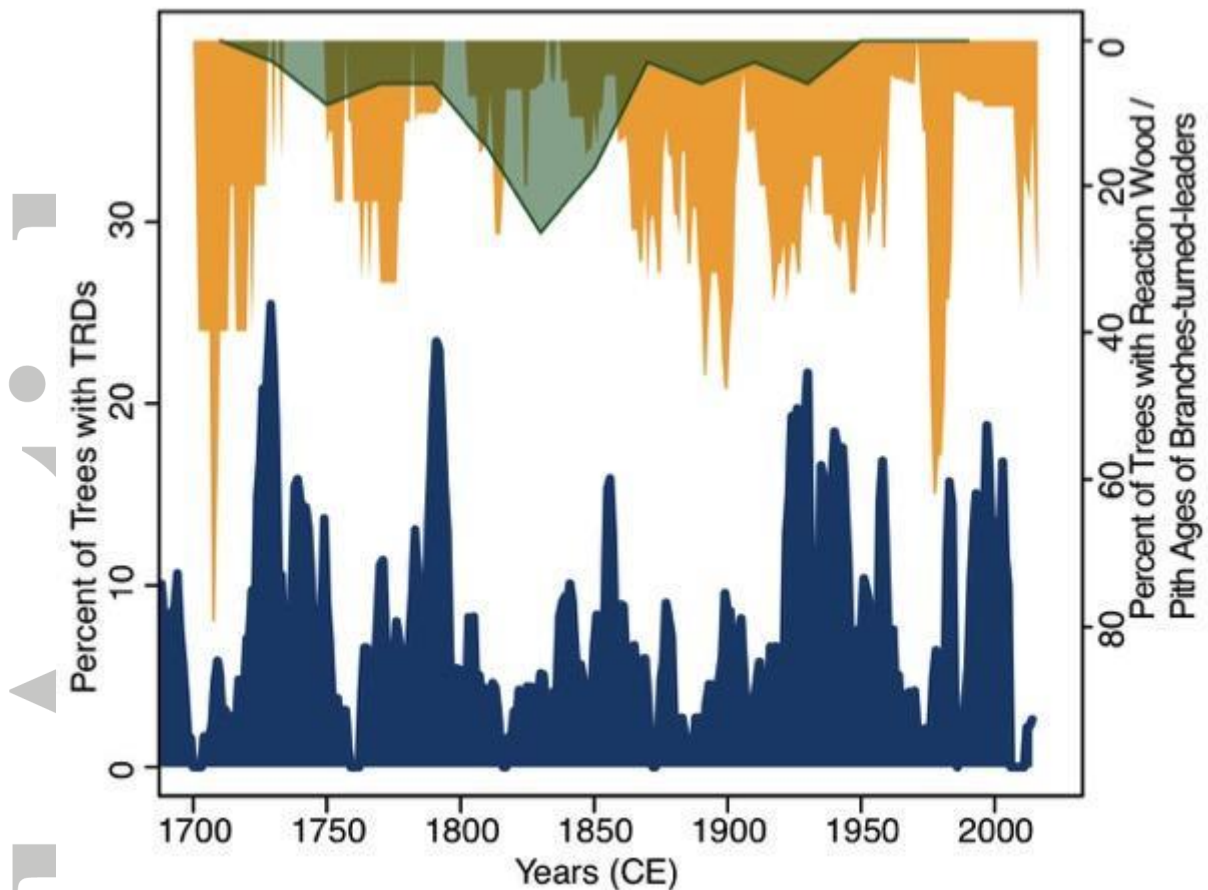


Figure 5. The alternating peaks of TRDs (blue), pith ages of replacement leaders (green), and reaction wood (orange) of replacement leaders ($n=38$; i.e. Figure 2) together form a consistent record of winter storm damage since CE 1700. TRDs record cambial damage during heavy ice storms. Pith ages on replacement leaders provide an age for when upturned branches grew upright and replaced a storm-damaged leader, probably during a time of deeper snowpack and lack of ice-storm damage. The timing of initial reaction wood in replacement leaders indicates when branches grew asymmetrically to regenerate into a leader. Reaction wood growth persists in leaders following damage from wind, snow, and ice coming from a predominant direction. In this case, asymmetrical growth was in response to southeasterly winds; Figure 2, 3).

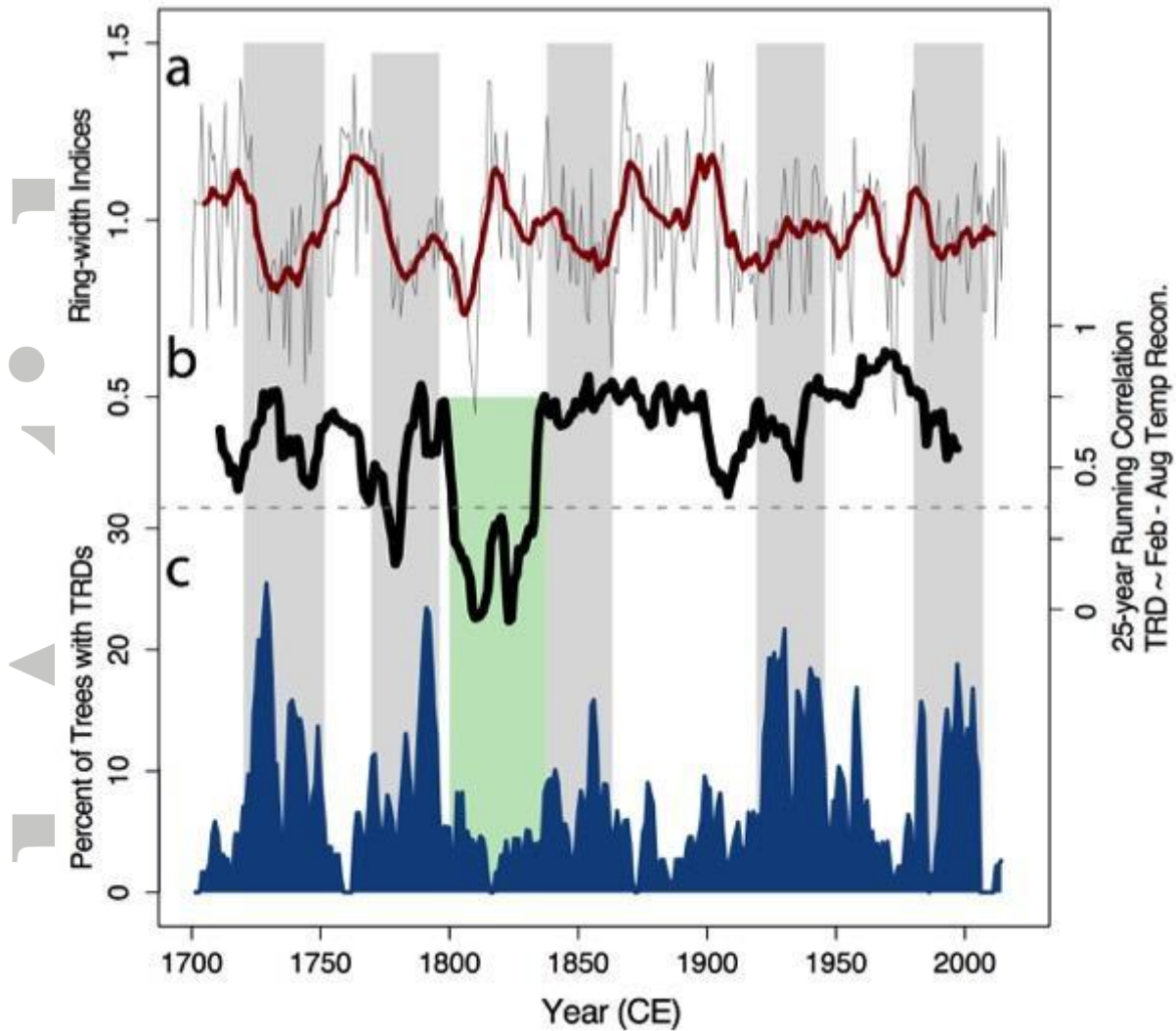


Figure 6. At these treeline sites, mountain hemlock's ability to prosper during warm springs and summers is compromised by damaging winter conditions. a) Peaks of TRDs (see c, highlighted in gray) are followed by smaller ring-width indices in the 200-year smoothing spline detrended storm-damaged chronology (gray line; 10-year moving average: red line). b) 25-year running correlations between the storm-damaged chronology and the regional Feb-Aug GOA temperature reconstruction [Wiles et al., 2014]. Storm-damaged divergence is particularly dramatic between CE 1800 and 1840, when most of the krummholtz trees elevated their canopies, probably in response to the protection afforded by deeper snowpacks (Figure 5).

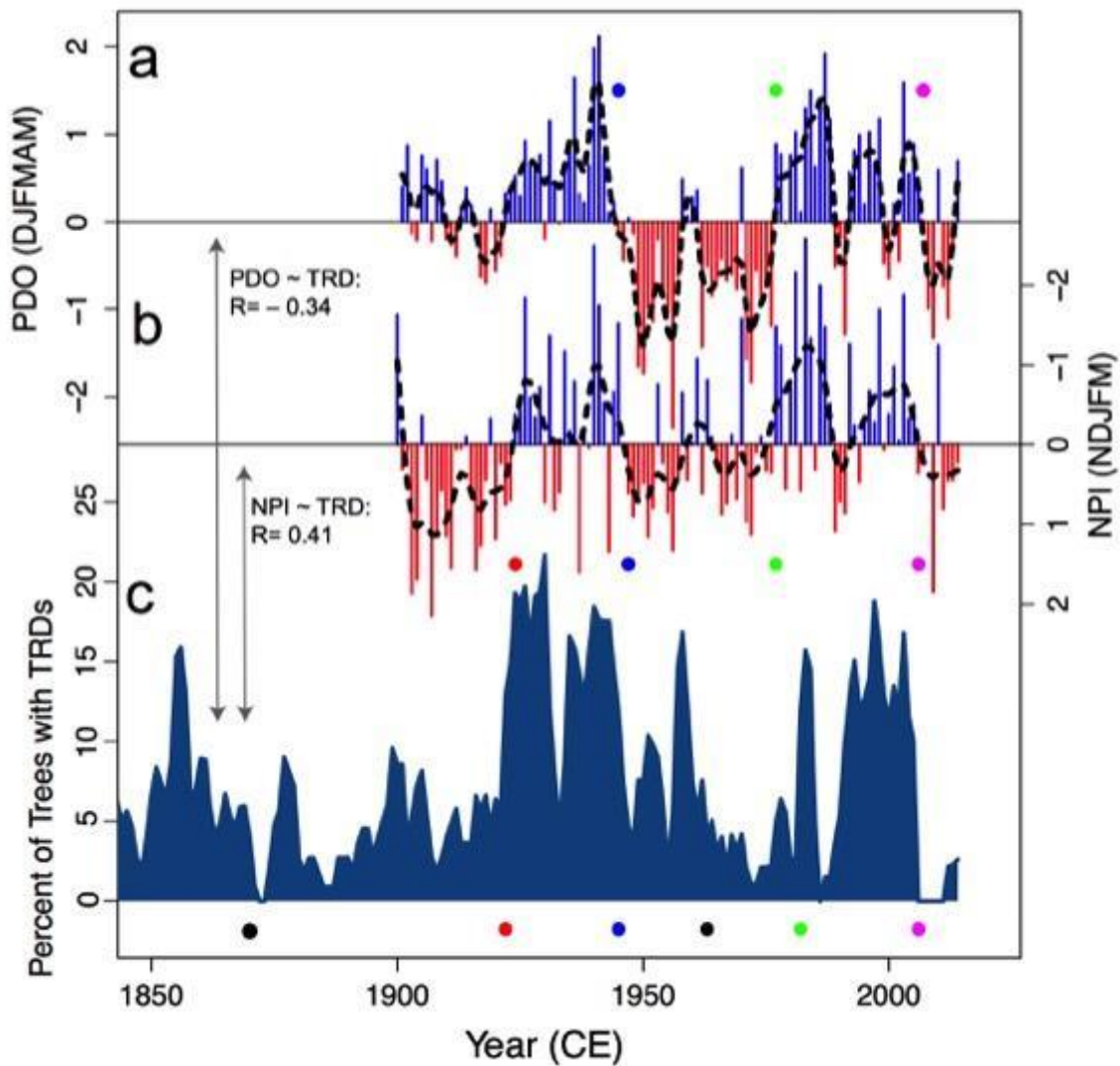


Figure 7. Rates of TRD production in treeline forests of Southeast Alaska (Panel c) are related to winter climate indices in the North Pacific region. Panel a) December-May mean PDO index. Panel b) November-March NPI (Aleutian Low index; AL). Correlations ($R=$) are Pearson's Correlation coefficients between the climate indices and the annual TRD record. Winters with stronger Aleutian Lows and more positive PDOs are accompanied by stormier winter conditions. Dots represent the timing of regime shifts for each time series based on Rodionov, [2004]. The same dot colors indicate a shared timing of regime shifts between TRDs and climate indices, where "shared" means they occurred within four years of each other, and shift in the same direction. Black dots below TRD time series are regime shifts either not registered or occur prior to the NPI or the PDO.